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Loïs Morel, B. Dujol, C. Courtial, M. Vasseur, B. Leroy, et al.. Spontaneous recovery of functional diversity and rarity of ground-living spiders shed light on the conservation importance of recent woodlands. *Biodiversity and Conservation*, 2019, 28 (3), pp.687. 10.1007/s10531-018-01687-3 . hal-02043736

HAL Id: hal-02043736

<https://univ-rennes.hal.science/hal-02043736>

Submitted on 25 Mar 2019

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**Spontaneous recovery of functional diversity and rarity of ground-living
spiders shed light on the conservation importance of recent woodlands**

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Abstract

Secondary (or recent) woodlands, whose development is favoured by massive farmland abandonment, are increasingly seen as promising habitats that limit losses of biodiversity and ecosystem processes. The importance of temporal forest continuity (i.e. the duration of an uninterrupted forest state) for conservation of the forest fauna has been demonstrated for several taxa, but its influence on functional diversity and conservation importance of communities remains unclear. We studied how temporal continuity can shape taxonomic and functional composition and structure of forest-ground spider communities at a regional scale. According to broad-scale ecological site characteristics, species composition and – to a lesser extent – trait distribution substantially diverged between ancient and recent forest sites. Yet, we found hardly any significant differences in functional β -diversity, community structure, or conservation importance between the two forest categories. The only difference was for functional originality, which quantifies the average functional uniqueness of species within an assemblage: spiders' communities of the ancient forests was more functionally original than those of the recent woodlands. Thus, in a conservation perspective, our study provides evidence that each forest harbours original species combinations, suggesting that each of them is irreplaceable, especially for ancient forests, which are functionally more original; however, recent woodlands have a high potential to spontaneously recover typical forest fauna communities with very similar structural and functional profiles to those of ancient forests.

Keywords

Arthropods; Farmland abandonment; Land use changes; Rewilding; Feral woodlands

Introduction

Land use change is considered as one of the major drivers of biodiversity changes in the terrestrial biosphere (Newbold et al. 2015). It can result in loss of both local and regional biodiversity (Sala 2000) or represent an opportunity for biological conservation through spontaneous rewilding (Pereira and Navarro 2015). Beyond modifications of species composition and structure of assemblages, these changes may affect ecosystem functioning (e.g. productivity, material cycling or resilience) by driving shifts of functional features of communities; e.g. by favouring the development of fast-growing plant species and thereby increasing ecosystem productivity (Allan et al. 2015). As a consequence, biodiversity conservation and related ecosystem processes are highly dependent on our understanding of the way historical and present land uses shape ecological communities. This is especially the case of mature ecosystems such as forest environments, which harbour high levels of biodiversity and numerous specialist species.

For centuries, regional species pools of woodlands have continuously been reshaped by successive periods of deforestation and reforestation (Kirby and Watkins 2015). These oscillations of the forest cover have brought about a profound dichotomy in forest landscapes, with coexistence of ancient forests and recent woodlands. In Western Europe, this trend increased in the last decades following massive abandonment of agricultural land resulting from socio-economical changes in developed countries (Renwick et al. 2013). Ancient forests are defined by the absence of a historical record of agricultural land use (and not as the absence of management) and have been continuously wooded for centuries (Hermy et al. 1999). Recent woodlands result from spontaneous processes of ecosystem de-domestication (Hermy and Verheyen 2007); they have been described as "feral" and are considered as novel ecosystems by several authors (Hobbs et al. 2013). This categorisation is not established yet (Miller and Bestelmeyer 2016; Murcia et al. 2014); it mainly relies on the importance of land-

use legacies (e.g. soil condition) that can lead to major differences in community composition and diversity between ancient and recent forests (see reviews by Hermy and Verheyen 2007; Spake et al. 2015).

In recent decades, there has been a growing effort to improve our understanding of forest fauna – including invertebrate taxa – responses to farmland abandonment (Bowen et al. 2007; Spake et al. 2015). In Europe, the key role of ancient forests for the conservation of arthropod communities has been demonstrated for carabid beetles (Assmann 1999; Desender et al. 1999; Goßner et al. 2008), saproxylic weevils (Buse 2011) and millipedes (Magura et al. 2015). Thus, although significant recovery of entomofauna has been noted in secondary woodlands (Queiroz et al. 2014), temporal forest continuity admittedly strongly influences species composition and richness of certain taxonomic groups through dispersal and recruitment limitations (Bowen et al. 2007; Spake et al. 2015).

Beyond these taxonomic differences, the functional responses of arthropod communities to forest continuity are still poorly understood when trying to determine whether recent woodlands can play a significant role in recovering biodiversity losses. Yet, by accounting for ecological differences among species, functional diversity may improve our understanding of ecosystem processes and functioning, e.g. community assembly or resilience (Cadotte et al. 2011). In this perspective, several indices have recently been developed to assess the functional structure and composition of ecological communities, such as functional richness, functional divergence, or functional redundancy (de Bello et al. 2007; Villéger et al. 2008). These indices complement taxonomic approaches by decomposing diversity into facets that provide insights into niche size and complementarity within communities (Pavoine and Bonsall 2011). Additionally, recent developments of trait-based ecology have demonstrated that other facets such as functional originality (related to uniqueness in trait combinations), specialisation (related to distinctiveness in trait combinations) and rarity (assessed using

species geographical rarity and trait rarity) were important to account for the ecology of outliers in conservation studies (Mouillot et al. 2013b; Violle et al. 2017): focusing on the conservation of functional diversity and rarity optimises biological feature preservation and decreases the probability of losing ecosystem functions (Leitão et al. 2016; Mouillot et al. 2013a). To further unravel forest fauna functional responses to temporal forest continuity, we developed an innovative approach based on spider communities. Spiders are one of the main ground-living predator arthropods. Thus, this group represents an important determinant of ecosystem functioning because spiders hold a key trophic position and regulate the soil biota both bottom-up and top-down. Moreover, contrary to taxonomic groups strongly dependent on a particular habitat (e.g. saproxylic organisms in old-growth forests) that are absent from pioneer ecosystems, their great diversity and abundance in numerous ecosystems makes them an excellent indicator of the way community structure is gradually reshaped by environmental change (Marc et al. 1999). Spider abundance and distribution are likely to change during reforestation strongly depending on vegetation structure and several other factors such as associated microclimate and litter architecture (Pearce and Venier 2006; Gallé et al. 2017). Therefore, shifts in environmental conditions during reforestation are expected to lead to variation in the composition and structure of ground-living spider assemblages (Ziesche and Roth 2008).

We analysed taxonomic and functional β - and α - diversity of ground spider assemblages in forest at a regional scale with three goals: (i) identify the main broad-scale factors that influence variations in the composition (so called β -diversity) of spider communities within a regional area; (ii) assess whether spider community structure (so called α -diversity) differs in ancient and recent forests, and (iii) assess whether spider community conservation importance also differs, using a combination of complementary α -diversity indices based on assemblage rarity and specialisation. We used a large regional spider database to perform, for the first

time to our knowledge, a comprehensive geographical assessment of taxonomic, structural, and functional comparisons of communities between ancient and recent forests at a broad regional scale.

Materials and methods

Study sites and dataset

We compiled data from a regional reference database including individual studies conducted in different environments in the Armorican Massif (western France) (see Leroy et al. (2013) for a presentation of the database). We extracted a subset of 56 spider assemblages sampled in forests from this database by applying a series of criteria (Fig. 1a). We selected only assemblages derived from plots of mesophilic oak-beech-dominated mature forest (for example, we avoided plantations and coniferous woodlands and young forests such as coppices), to limit the influence of environmental heterogeneity and stand maturity. These plots were homogeneous sets of ~ 1 ha corresponding to management units and were distributed in 16 sites across the regional area (Fig. 1, Online Resource 1). Then, we retained sites larger than 10 ha to avoid areas in which assemblages could be strongly influenced by edge effects. This selection resulted in 56 sites composed of one to six plots separated by 0.1 Km to 2 Km (Online Resource 1). Within-site distances were always smaller than inter-site distances, which ranged from 5 Km to 200 Km. Then, we set apart spider communities of ancient forests from those of recent woodlands by checking the temporal forest continuity of each forest site using Cassini map layers (year 1790) and the Napoleonic cadastre (year 1847). These two historical land-use documents allowed for a precise spatialisation of ancient forests in France. We defined ancient forests as sites already forested in the middle of the 18th century, when the overall forested area was at its minimum over the French territory (Cateau et al. 2015). Hence, ancient forests are plots that have had an uninterrupted forest state for at

least 220 years. Here we assume that temporal forest continuity as the absence of a historical record of agricultural land use and not as the absence of management, such as logging (Hermý and Verheyen 2007). We defined recent woodlands as forests resulting from afforestation during the 20th century, i.e. no more than 120 years old. Thus, our dataset included 12 ancient forests (n plots=37) and 4 recent woodlands (n plots=19). Such an unbalanced design illustrates that even if farmland abandonment is an important phenomenon in Brittany, it has rarely led to the emergence of large, contiguous wooded sites. However, the recent woodlands were well distributed within study area: each of the four geographical sets of sites contained a recent woodland (Online Resource 1). Each of them are located less than 3 km from an ancient forest (at least a small patch). Finally, we filtered collections to retain only standardised sampling protocols based on pitfall traps and focused on forest-ground spider communities. In each plot – the experimental unit –, the local species pool was compiled from 3 pitfall traps spaced 10 m apart and all situated at the center of the plot. Collections were carried out from April to June (a period corresponding to the peak of spider activity in the region) of 2013, or 2014, or 2015 (see details on sampling methods in Online Resource 2). Species abundance values were standardised according to the number of days a trap was active, to account for the effect of trap disturbance. The final dataset included 5,719 adult individuals belonging to 110 spider species collected in the 56 plots.

Environmental variables

We considered nine environmental variables to characterise biogeographical, climatic, historical, and broad-scale ecological conditions at the regional scale: geological substrate (4 categories: Granite rock, Sandstone, Schist or Volcanic rock), temporal forest continuity (2 categories: ancient or recent), site area (Ha), latitude, longitude, temperature maximum in 2015 (degree Celsius), mean annual rainfall (mm), number of hours of solar radiation for the

1997-2006 period, and altitude (m). We compiled them from data from the French National Geographic Institute (www.geoportail.fr) and the French weather forecast institute (www.meteofrance.fr).

Data analyses

Sampling effort: site richness and completeness

We first analysed the robustness of our dataset by assessing the completeness index composed of the observed richness divided by estimated species richness (Soberón et al. 2007). We calculated three richness estimators (Chao2, Jackknife 1, and Incidence Coverage-based Estimator (ICE)) commonly applied on similar datasets (Hortal et al. 2006; Soberón et al. 2007). We calculated completeness indices for the whole dataset, for a subset composed of ancient forests and another composed of recent woodlands, and for each of the 16 sites. Richness estimators were computed with the “fossil” R package (Vavrek and Vavrek 2011).

From life-history traits to functional distance between species of the regional pool

We selected a set of five life-history traits available in the literature to describe the functional features of the 723 spider species recorded in the regional database. Seventy-eight species whose trait values were not available in the literature were excluded from our analyses. Traits were chosen to obtain a multidimensional representation of functional features of spiders describing the main facets of their ecology: body size (continuous: maximum size of females ; log-transformed to reach more symmetric distribution ; Roberts 1995), feeding guild (7 categories: ambush hunters, ground hunters, other hunters, sheet web, space web, orb web, wandering web), daily activity (3 categories: diurnal, nocturnal, both) (Cardoso et al. 2011), phenology (4 categories: spring, summer, autumn-winter, eurychron) and stratum utilisation (2 categories: ground-dwellers, vegetation-dwellers) (Harvey et al. 2002). Body size

influences a wide range of ecological and physiological characteristics of a species (e.g. locomotion, space use, life history) and strongly affects resource use (Brose et al. 2006). Feeding guilds, phenology, stratum utilisation and daily activity are linked to resource partitioning among species and permits to analyse resource-use strategies across different sites.

To measure functional α - and β -diversity, we used euclidean-space-based approaches which represent the extent of niche space exploited by communities by simultaneously accounting for several traits (Fig. 1b). We built a multidimensional functional space based on the trait values of all species retained for our analyses (i.e. 645 species including all 110 species observed in our dataset of woodland communities; Online Resource 3). Because most traits were categorical, we performed a principal coordinates analysis (PCoA; with Cailliez's correction based on a Gower dissimilarity matrix computed on species traits (Villéger et al. 2008). To find the best multidimensional space possible, we used the mean-squared deviation (mSD) criterion that measured how faithfully the initial functional distances (based on trait values) were represented in the final multidimensional PCoA-based space, as recommended by Maire et al. (2015). The lower the mean-squared deviation, the higher the quality of the functional space. We thus kept 4 dimensions for the functional space (mSD = 0.008). All functional indices were then calculated for both α - and β -diversity within this functional space (Fig. 1c-d).

Taxonomic and functional composition of communities: insight into overall β -diversity patterns

To quantify plot-to-plot compositional variation *within* and *between* the two forest categories, we measured pairwise dissimilarities between each pair of plots (i.e. the 56 assemblages retained after selection from the global database; Fig. 1) with Jaccard's index for the

taxonomic facet and Jaccard-derived dissimilarities for the functional facet (Villéger et al. 2013). Functional β -diversity is based on the calculation of the ratio between unshared functional space and the total functional space filled by communities in the multidimensional space (Villéger et al. 2013). In addition, we assessed the contribution of a strict turnover within taxonomic and functional β -diversity, following the frameworks of Baselga (2010) and Villéger et al. (2013), respectively. The turnover index was independent of differences in species richness (Leprieur and Oikonomou 2014), so we strictly focused on species and trait turnover in β -diversity changes. β -diversity metrics were calculated using the “betapart” R package (Baselga and Orme 2012).

Taxonomic and functional structures of communities: insight into α -diversity patterns

Community structures were first investigated through three taxonomic diversity indices: species richness, species abundance and – to better understand the response of traditional taxonomic indices to temporal continuity – Pielou’s evenness (which measures the evenness of abundance distribution among species). All indices that include abundance were based on standardised abundance, i.e. a continuous variable (see Table 1). To assess the functional structure of each community, we computed multivariate indices of functional diversity that measure functional distances of species from the volume of convex hull intersections in the multidimensional space. Thus, for all 110 species listed in the global species-by-site matrix, species coordinates in the overall multidimensional space were extracted to measure two complementary facets of functional diversity for each assemblage (Fig. 1c): functional richness (FRic) and functional divergence (FDiv) (Villéger et al. 2008). Furthermore, we estimated the functional redundancy (FR) of each assemblage by using the framework of de Bello et al. (2007) which measures FR as the difference between species diversity and Rao’s quadratic entropy based on their functional dissimilarity (see Table 1 for metric details).

Finally, to quantify shifts in trait distribution, we also computed community-weighted mean trait values (CWM) and the proportion of presence-absence in each category for categorical traits, using the “FD” package in R (Laliberté et al. 2014).

Taxonomic and functional conservation importance: insight into patterns of rarity, specialisation and originality of spider communities

We used the entire regional reference database to compute conservation importance analyses; hence, the importance of each forest category was assessed with the regional species pool (i.e. the 645 species retained for our analyses; (Fig. 1d)). Concerning the taxonomic facet, we used the Index of Relative Rarity (I_{RR}) of Leroy et al. (2012). The I_{RR} is the average rarity level of each species assemblage, based on species rarity weights. Rarity weights are calculated with regional occurrence data, so that rare species are species geographically rare in the entire region. We calculated rarity weights with a method that can be adjusted according to a user-chosen rarity cut-off point (Leroy et al. 2012; 2013). This method assigns rare species rarity weights that increase exponentially when their occurrence falls below the rarity cut-off point. To ensure that the chosen cut-off would be sufficient to distinguish rarity patterns among assemblages, we defined cut-offs following the guidelines of Leroy et al. 2012: the rarity cut-off was defined as the occurrence level at which the average proportion of rare species in local assemblages was 25% (see Discussion in Leroy et al. 2012). The I_{RR} of a species assemblage was calculated as the average rarity weight of all the species of the assemblage, and subsequently normalised between 0 and 1. We used the “rarity” package (Leroy 2016) for these analyses.

Concerning the functional facet, we first used the recent framework proposed by Violle et al. (2017) to measure the functional rarity (FRar) of each assemblage. At a regional

scale, this index is based on the two main components of species rarity (Violle et al. 2017), namely taxonomic restrictedness (R_i ; regional-scale characteristic of a geographically restricted species) and functional uniqueness (U_i ; regional-scale feature of a species possessing unique traits). We applied the additive framework that combines regional taxonomic restrictedness and functional uniqueness. Thus, FRar of species i was estimated as the addition of R_i and U_i for each species recorded in the regional dataset. Finally, FRar of species from woodland assemblages were summed and then divided by species richness so that the index depended on rare species proportions but not on species richness.

Finally, we completed the assessment of forest continuity for conservation by assessing functional specialisation (FSpe) and originality (FOri) of communities. We used two multidimensional indices implemented through the framework of Mouillot et al. (2013b), which assesses the functional features of each local community in view of the species pool; see Table 1 for metrics details).

Statistical significance tests

Given the dependent structures of the dataset, we systematically integrated random effects into models to provide unbiased statistical significance tests. The chosen model structures account for hierarchical and/or spatial structures of the sampling design and make it possible to effectively avoid potential biases due to pseudoreplication (Davies and Gray 2015). Therefore, in each model (whether β - or α -diversity), we defined the spatial structure with *regional provinces* grouping nearby sites (see Online Resource 1) and the hierarchical structure (sampling plots nested within *study sites*) as random effects.

To analyse patterns of β -diversities, we applied permutational multivariate analysis of variance (PERMANOVAs) on dissimilarity matrices (i.e. on the previously calculated Jaccard index and Jaccard-derived dissimilarities) to check whether assemblages differed according to

sites ('site effect') and to temporal forest continuity ('ancientness effect'). Then, still based on the same taxonomic and functional dissimilarity matrices, we performed principal coordinate analyses (PCoA) to visualise β -diversities and highlight the structure of the species-by-site dataset (i.e. the 56 assemblages). Finally, to interpret PCoA patterns, the nine environmental variables were fitted onto ordinations. For each variable, we evaluated the significance of the explanatory power with a Monte-Carlo randomisation test (9,999 permutations), and the link strength with ordinations, using the squared correlation coefficient. For both PERMANOVAs and environmental interpretations of the PCoA, random effects were integrated by restricting permutations between *regional provinces* and between *sites* to account for the spatial and hierarchical structures of the dataset, respectively. These analyses were treated with the "vegan" and "permute" R packages (Oksanen et al. 2017; Simpson et al. 2016).

To analyse patterns of α -diversity, we tested the means of each continuous metrics (i.e. FRic, FOr) in ancient *versus* recent woodlands with linear mixed-effect models (LMMs). For species richness, which is a discrete variable, we used generalised linear mixed-effect models (GLMMs). For all models, temporal forest continuity was defined as a fixed effect, and *regional provinces* and *sites* as random effects. We log-transformed values of standardised abundance, I_{RR} , FOr and FSpe to improve model fitness. We used the "lme4" package (Bates et al. 2015) for these analyses.

All data analyses were performed using R version 3.4.1 (R Core Team 2017).

Results

Sampling effort: site richness and completeness

On average, 19.01 ± 5.57 (mean \pm sd) species were sampled per site, ranging from 13 to 47. The mean value of the three selected completeness estimators for the overall dataset was

relatively high (0.83 ± 0.04), suggesting that the information extracted from the database gave us a fairly satisfactory picture of the species composition of the spider communities observed in the forest environments we studied (Online Resource 4). Out of the 16 sites, two (Rennes, Stangala) displayed low values (0.65 and 0.66, respectively), and four others had no estimable values because the number of samples was too low (Bois du Chap, Cranou, Menez, and Sœuvres).

Regional patterns of taxonomic and functional dissimilarities

Pairwise dissimilarities of spider assemblages were high and quite similar (they ranged from 0.66 to 0.74 for the taxonomic facet and from 0.76 to 0.82 for the functional facet across the entire study area, *within* and also *between* the two forest categories (Table 2)). In each case, pairwise functional dissimilarities were greater than taxonomic ones. However, when variation in species richness was controlled by focusing on the contribution of turnover to pairwise dissimilarities, functional variations were systematically lower than taxonomic variations (from 0.40 to 0.46 and from 0.56 to 0.67, respectively).

Sources of variation in taxonomic and functional dissimilarity

PERMANOVA results highlighted significant differences in the taxonomic composition of spider communities across the 16 forest sites and between the two forest categories. The “site” factor explained more than half of overall variance in the regional area ($R^2 = 0.518$; $p = 0.001$) whereas the “temporal forest continuity” factor explained around 1/10 ($R^2 = 0.096$; $p = 0.001$). PERMANOVAs applied to functional composition also highlighted significant differences across the 16 forest sites ($R^2 = 0.38$; $p = 0.001$). Differences were likewise significant between the two forest categories, but the part of the explained variance was very low ($R^2 = 0.034$; $p = 0.01$).

Our analyses of the taxonomic facet showed a strong separation between spider communities of ancient and recent forests on the PCoA (Fig. 2). Regardless of their geographical position, the communities sampled in the recent woodlands were all more similar to one another than they were to their geographic neighbours from ancient forests; and the reverse was true for ancient forest communities (Fig. 2; Online Resource 1). Thus, when the influence of the temporal forest continuity was analysed through the fitting of environmental variables within the ordination space, it appeared as one of the main factors leading to the taxonomic compositional variation within the regional area ($r^2 = 0.35$, $p = 0.001$; Table 3). Additionally, PCoA revealed that the taxonomic composition was also strongly influenced by the geographical locations and climatic conditions of the sites: on the one hand, spider communities clearly and strongly differed according to altitude and latitude ($r^2 = 0.58$ and $r^2 = 0.54$, respectively; Fig. 2; Table 3); on the other hand, the composition of spider communities was also significantly (but more slightly) correlated with solar radiation and longitude ($r^2 = 0.34$ and $r^2 = 0.20$, respectively; Fig. 2; Table 3). Among the other four variables, “area of sites”, “rainfall” and “geological substrate” also had an influence, but to a much lesser extent ($r^2 < 0.15$), while “temperature” was not significant.

Our analyses of the functional facet suggest that spider communities of recent and ancient forests were not distinguishable on the PCoA (Fig. 2). Only longitude and temperature were significantly correlated with the ordination ($r^2 = 0.18$; $p = 0.01$ in both cases; Table 3).

The two-axis PCoA performed at the taxonomic level summarised 21% of the variance of the Jaccard dissimilarity matrix, but the pairwise distances plotted onto the ordination space were proportional to the observed ones (indicated by the fact that the cloud of points approximately followed a straight line; see Shepard diagram in Online Resource 6). Concerning the functional facet, the PCoA summarised a larger part of the variance (28%), but less accurately so (Online Resource 6).

Community structure and conservation importance

The mean values of all the metrics describing community structure at the taxonomic (species richness, standardised abundance, evenness) and functional (functional richness, divergence, redundancy) levels did not differ between ancient forests and recent woodlands (Wald's test; $p > 0.05$; Fig. 3; Online Resource 5). Similarly, the metrics describing taxonomic (I_{RR}) and functional (FRar) rarity in the two forest environments did not differ, nor did functional specialisation (Wald's test; $p > 0.05$). In contrast, average functional originality of ground-living spider communities was significantly higher in ancient forests than in recent woodlands (Wald's test = 12.9; $p = 0.0003$) (Fig. 4; Online Resource 5).

Additionally, several mean trait distributions (assessed with CWMs) showed significant differences between ancient and recent forests (Fig. 5; Online Resource 5). Thus, mean body size, the proportion of species carrying out their life cycle in autumn/winter, and the proportion of various hunters (called *other hunters*) were significantly higher in the communities of ancient forests (Wald's test = 4.75; $p = 0.03$); the proportion of ground hunters was marginally higher in the ancient forests (Wald's test = 3.6; $p = 0.056$). On the other hand, there were significantly more orb-web and space-web spiders as well as more vegetation-dweller species in the recent woodlands than in the ancient forests (Wald's tests = 4.3, 8.9, 16.9; $p = 0.04, 0.003, < 0.0001$, respectively); the proportion of species active both in the daytime and at night was marginally higher in the recent woodlands (Wald's test = 3.7; $p = 0.053$). Nine out of the 16 investigated traits did not show any differences between the two forest categories.

Discussion

Based on the available data at a regional scale, our study provides new insights into the ecological specificity of ancient and recent forests by comparing taxonomic and functional β -

and α -diversity of ground-living spider assemblages. We obtained three main findings. First, taxonomic and functional composition of spider communities greatly varied within the study area, with lower biotic homogeneity at a regional scale than we expected. Second, we observed significant differences in species composition and trait distribution between ancient and recent forests. On the other hand, β -diversity converged when the composition was characterised from a functional point of view (the extent of trait distribution, not their mean). Third, the community structure and conservation importance of the two forest categories did not reveal significant differences, except for functional originality.

Compositional specificity of forest sites within the regional area

We found strong plot-to-plot variations (β -diversity) in taxonomic and functional composition within and between the forests (Jaccard dissimilarities > 0.7 , Table 2). In addition, the relative part of strict functional turnover was lower than the taxonomic one (0.44 and 0.61, respectively; Table 2). This interesting finding suggests that species replacement did not systematically lead to a shift in functional composition and suggests probable trait redundancy in spider communities inhabiting forest environments in our region.

These compositional differences – especially taxonomic ones – were strongly linked to site identities (see PERMANOVA results). This result suggests that each forest site exhibited to some extent an original composition of ground-living spider communities, and, to a lesser extent, distinct combinations of life-history traits. Temporal forest continuity appeared as one of the major factors explaining taxonomic β -diversity among spider communities; this was especially represented by one of the two major axes of taxonomic compositional variation within the regional area (Fig. 2). In addition, other environmental characteristics of the sites (altitude, latitude, solar radiation, longitude) also significantly influenced global dissimilarity and represented the second major axis of taxonomic compositional variation. We thus found

that the main sources of taxonomic and – to a lesser extent – functional β -diversity were the geographical positions of the forests within the regional area, i.e. the longitudinal and latitudinal coordinates of the sites as well as their altitudes (Table 3). Combined with the other geographical differences in parameters such as rainfall, temperature, or solar radiation, the strong effects of these variables suggest a great influence of broad-scale climatic conditions on the regional β -diversity of forest spider communities. These results are consistent with our knowledge of niche properties of spiders that are conditioned by the interplay of a few abiotic factors strongly linked to climatic conditions, namely shading and moisture (Entling et al. 2007).

A secondary significant source of taxonomic β -diversity was the geological substrate. Thus, although we restricted our investigations to one forest type (i.e. oak- and beech-dominated woodlands), this finding may suggest that our dataset included contrasting vegetation types and physiognomies linked to geological substrates and, as a corollary, distinct spider communities. Plant community composition indeed strongly influences arthropod assemblages, including predators, because of numerous causal factors (e.g. vegetation structure, predator-prey interactions, microclimatic conditions) that affect invertebrate distribution (Schaffers et al. 2008). The surface area of sites also captured a significant part of the variance of taxonomic dissimilarities, suggesting that site periphery influenced species composition. Landscape structure influences the composition of spider assemblages because it drives the availability of surrounding habitat sources (Öberg et al. 2007) and edge habitats (Pearce et al. 2005). More specifically, smaller forest patches could be occupied by open-habitat specialist spiders absent in large forests because their high edge-to-area ratio favours an edge effect and individual moving (Gallé 2008).

Beyond these significant relationships between β -diversity and sites broad-scale ecological characteristics, a large part of overall taxonomic and functional β -diversity

remained unexplained (48% of total variance, see PERMANOVA results). A first explanation could be linked to fine-scale ecological parameters that we did not evaluate (e.g. see Pinzon et al. 2018), and which could lead to environmental heterogeneity of forest biota. Several factors can affect spider community composition, such as vegetation structure, litter architecture, or such as micro-climate, soil moisture, soil type, organic matter content, pH, fertility, as well as management practices (see Prieto-Benítez and Méndez 2011; Schaffers et al. 2008). A second explanation may arise from stochastic processes such as probabilistic colonisation (Mallis and Hurd 2005) or historical contingencies. The ranking and timing of species immigration during colonisation processes, known as priority effects, can also affect local occurrence and abundance and may generate various patterns of species composition (Fukami 2015). Finally, temporal fluctuations of the abundance of spider populations affect their detectability and may also influence the geographical patterns observed in species composition (Gossner et al., 2014). This could increase differences among communities when comparisons are based on results of pluri-annual field surveys. In this context, it would be interesting to complete our investigations by a study integrating a longer sampling period that would smooth out the potential phenological variations across sites.

Trees do not make forests: major differences in taxonomic composition, and shifts in trait distribution between ancient and recent forests

Our findings provide clear evidence that taxonomic composition of ground-living spider communities significantly differs between ancient and recent forests. Spider communities sampled in the same type of forest were more alike than spider communities sampled in different types of forest, regardless of their geographical positions. On the other hand, we did not find any difference in functional β -diversity between forest categories; but we found significant differences in the life-history trait distributions (Fig. 2; Fig. 5). Altogether, these

473 results are consistent with our expectations that forest continuity leads to ecological
474 differences between woodlands and in turn generates various compositional patterns by
475 affecting spider niche properties. It is now well known that recent woodlands differ
476 ecologically from ancient forests (see the review by Hermy and Verheyen 2007). These
477 ecological differences are mainly due to agricultural legacies that may sometimes strongly
478 and lastingly impact soil properties such as pH, organic matter, carbon/nitrogen/phosphate
479 contents, and in turn pedofauna and vegetation composition (Dupouey et al. 2002; Flinn and
480 Marks 2007). Changes in soil physicochemical properties and associated food webs (i.e.
481 brown and green food webs) in turn affect upper trophic levels such as arthropod predators by
482 influencing local microclimates, habitat structure or prey availability (Pearce and Venier
483 2006; Ziesche and Roth 2008). As a consequence, given the weak dispersal abilities and the
484 strong association of forest specialist arthropods to micro-habitats and physical conditions of
485 woodlands (i.e. moisture and shadow), their potential establishment in recent re-growth
486 forests needs time (Bowen et al. 2007; Spake et al. 2015). This greater proportion of
487 specialised species (occupying a restricted niche) in ancient forests is especially illustrated in
488 terms of traits by the overrepresentation of species that carry out their life cycles in
489 autumn/winter as compared to recent woodlands (Fig. 5). This was the case for *Centromerus*
490 *brevipalpus* or *Hahnia ononidum*, two strictly forest-dwelling spiders (Online Resource 3,
491 Online Resource 7). Otherwise, these compositional differences between the two types of
492 forests may also result from the temporary maintenance of species associated to earlier
493 successional stages in recent woodlands. We indeed observed that values or categories of life-
494 history traits that can favour the colonisation of new habitats were better represented in recent
495 forests than in ancient forests. These traits included a small size, generalist traits such as large
496 daily activity (both diurnal and nocturnal), or membership in hunting guilds primarily using
497 webs (Fig. 5), because such traits make species more prone to dispersal (ballooning) and less

dependent on the soil biota (Nentwig 1986; Gobbi 2017). This is typically the case of the Lynxyphiidae family. Moreover, temporal continuity could interact with stand maturity and cause variations in species composition (Janssen et al. 2017). Thus, although we carefully selected forest plots with similar maturity, a few compositional differences may have been related to structural attributes such as dead-wood material or litter complexity, which also influence spider distribution (Buddle 2001; Bultman et al. 1982). This is the case for some species more specifically found under dead wood stumps or forest floor stones (e.g. the large cribellate spider *Amaurobius similis* or the sheet-weaving spider with tubular retreat *Eritagena picta*). Future investigations should account for this distinction and refine our understanding of the influence of forest continuity on spider community structuring. Finally, some of these compositional differences may not be linked to deterministic factors: as predicted by the theory of community assembly, stochastic forces such as historical contingency (e.g. priority effects) or neutral processes such as dispersal and ecological drift may interact with environmental filtering and biotic interactions to shape communities and partly result in unpredictable assemblages (Chase 2003; Fukami 2015).

Trees make forests: convergence of community structures between ancient and recent forests

Despite differences in taxonomic composition and trait distribution, functional β -diversity, community structure and conservation importance were highly similar in the two forest categories. A first consequence is that the degrees of functionality ensured by spider communities in both ancient and recent forests seemed unchanged: functional richness suggests that niche sizes (i.e. the volumes of functional space) exploited by spider communities were identical (Fig. 3a-b). Furthermore, the consistency of abundance values and the high values of Pielou's evenness index suggest that ecological niches were exploited

with the same intensity, i.e. species shared available resources similarly in ancient and recent forests (Fig. 3c-e). The lack of differences in functional divergence shows that the degrees of niche differentiation in the communities were also similar (Fig. 3d) (Mouchet et al. 2010; Villéger et al. 2008). Additionally, the same levels of functional redundancy suggest that spider species performed similar functions in the two forest categories and were therefore interchangeable, with little impact on ecosystem processes (Fig. 3f) (Fonseca and Ganade 2001). The low I_{RR} values revealed that the communities of the ancient and recent forests were dominated by species otherwise widespread in western France. Moreover, ancient forests did not harbour communities with rarer functional features than recent woodlands relatively to the regional area (Fig. 4a-b). Similarly, functional specialisation of forest spider communities did not differ over time, suggesting similar widths of the ecological niches exploited by spiders in all forest environments (Fig. 4d). Previous studies investigating biodiversity responses to farmland abandonment found that fauna taxonomic structure in secondary forests could rapidly resemble fauna taxonomic structure of ancient forests (Bowen et al. 2007; Spake et al. 2015). More precisely, no difference in α -diversity between ancient and recent forests was found in communities of ground-living beetles (Assmann 1999) and spiders (Hurd and Fagan 1992) in temperate ecosystems. By highlighting similar trends with functional metrics, our results are in line with research showing that recent woodlands can spontaneously recover forest fauna weakly impeded by dispersal constraints, including many arthropod groups (Nordén et al. 2014; Queiroz et al. 2014). Finally, these results raise the important question of which conditions generate such rapid and spontaneous recovery of structures of ecological communities. Can these processes also be observed after the abandonment of agrosystems intensively exploited during the 20th century?

In contrast with these similarities between the two forest categories, we evidenced that ancient forests harboured functionally more original assemblages (Fig. 4c). A first potential

consequence is that ancient forests tend to harbour on average more functionally original species than recent woodlands do. In other words, species of ancient forests seem to be isolated within the functional space of the regional species pool. Among these species, several are known to be specific to habitat conditions more frequently found in ancient forests. For example, *Neon reticulatus* or *Saloca diceros* are two small litter-hunter specialist species generally associated with a dense leaf litter, exhibiting one of the most important values of functional originality, and only recorded in ancient forests (Online Resource 7a; Online Resource 3). Yet, there were also other species exclusively present in recent woodlands which showed high degrees of functional originality as well as analogous functional features to those exclusively present in ancient forests. For example, *Nerience clathrata* and *Linyphia hortensis* are two small sheet web linyphiidae observed exclusively in ancient forests and recent woodlands, respectively (Online Resource 7a; Online Resource 3). This result, combined with the fact that exclusive species are rare (Online Resource 7a), suggests that differences in species composition were not the only parameter explaining the mean differences in F_{ori} between the two forest categories. The higher F_{ori} of the spider communities of ancient forests likely also resulted from the greater representation (in terms of abundance) of functionally distinct species (e.g. forest specialists such as *Apostenus fuscus* or forest generalists such as *Pardosa saltans*; Online Resource 7a). Overall, whether in terms of species distribution or abundance, the most original forest spiders appear to be favoured in ancient forests, either because temporal continuity allows for the maintenance of populations over time, or because habitat conditions are better suited to their biological cycles. The fact that functional original spiders might be favoured in ancient forests is an interesting finding because it provides functional perspectives to previous works highlighting the importance of ancient forests to preserve highly stenoecous and relict arthropod species (Assmann, 1999; Buse, 2012).

Study limitations

Despite our efforts to improve the reliability of our dataset and the robustness of the analyses, our results should be interpreted considering the methodological limitations inherent to large datasets compiling different individual studies. Our main limitation lies in the fact that our design was unbalanced, with a larger number of plots sampled in ancient forests than in recent woodlands ($n=37$ vs. $n=19$). This imbalance was reflected in the lower global completeness value of recent woodlands, suggesting that these communities were sampled less accurately, even though two of the three estimators had similar values to those of ancient forests (Online Resource 4). In addition, most sites, whether ancient or recent, had relatively high completeness (> 0.75). Nevertheless, this imbalance may have influenced both metrics related to geographic rarity (I_{RR} , $FRar$) because of a greater probability to detect rare species in ancient forests than in recent woodlands. However, this bias seemed to have little influence on our results: spider communities of ancient forests did not show higher values for I_{RR} or $FRar$ (Fig. 4a-b), and their variances were homogeneous between the two forest categories (F test = 1.66, 1.87; $p = 0.25, 0.16$, respectively; $df_{num.} = 36, df_{den.} = 18$). These results suggest that, even with fewer pitfall traps, the distribution of these rarity values in the recent woodlands was similar to that of ancient forests. However, we consider our study as a first approach to examine the response of forest spider assemblages to farmland abandonment. This first approach is paving the way for future works based on more exhaustive data (both in terms of time and space), which will also account for fine-scale ecological parameters (e.g. abiotic soil conditions) and finer life-history traits, and complete our results. Overall, we feel that a collective research effort focusing on spontaneous rewilding would be welcome to assess to what extent and under which conditions recent afforestation may significantly contribute to the conservation of forest arthropods.

598 **Concluding remarks**

599 The present study shows that, combined with broad-scale ecological factors, temporal
600 continuity contributes to generate various assemblages among forest sites. In a conservation
601 perspective, this is an interesting result because it demonstrates that each forest, whether
602 ancient or recent, is not equivalent and contributes to regional biodiversity. Thus, our results
603 suggest that ground-living spider communities of ancient forests are irreplaceable because of
604 their compositional uniqueness and high functional originality. However, by showing that
605 communities with structural and functional profiles very similar to those of ancient forests can
606 be recovered within a century, our results also highlight the promising conservation role
607 possibly played by recent woodlands in times of global land-use changes.

608

609 **Acknowledgements**

610 This work was supported by the ‘Région Bretagne’, ‘Conseil départemental des Côtes
611 d’Armor’, ‘Conseil départemental Finistère’, ‘Conseil départemental d’Ille et Vilaine’,
612 ‘Conseil départemental du Morbihan’ and ‘Communauté de communes de Plouha-Lanvollon’
613 for technical and financial support. Moreover, we also would like to thank the military camp
614 of St-Cyr-Coëtquidan and especially Alexandra Baudart and Sébastien Gautier (ONCFS) as
615 well as Nicolas Le Deuff, Guy Le Reste (ONF) and David Rolland (FDC 22) for their help in
616 acquiring data. We are also very grateful to the many colleagues and friends who helped in
617 the preparation, analysis and treatment of data: Simon Chollet, Pierre Devogel, Maxime
618 Hervé, Vincent Jung, Jean-Paul Lechapt, Margot Morin, Melaine Roullaud and Manon
619 Simoneau, as well as the three anonymous reviewers for their careful reading of our
620 manuscript and their many insightful comments and suggestions. We are also very grateful to
621 Diane Morel for the two drawings included in Figure 2.

References

- Allan E, Manning P, Alt F, Binkenstein J, Blaser S, Blüthgen N et al. (2015) Land use intensification alters ecosystem multifunctionality via loss of biodiversity and changes to functional composition. *Ecol Lett* 18: 834–843.
- Assmann T (1999) The ground beetle fauna of ancient and recent woodlands in the lowlands of north-west Germany (Coleoptera, Carabidae). *Biodivers Conserv* 8:1499–1517.
- Baselga A (2010) Partitioning the turnover and nestedness components of beta diversity. *Global Ecol Biogeogr* 19: 134–143.
- Baselga, A, Orme CDL (2012) betapart: an R package for the study of beta diversity. *Methods Ecol Evol* 3: 808–812.
- Bates D, Maechler M, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects Models Using lme4. *J Stat Softw* 67(1): 1–48.
- Bello F, Lepš J, Lavorel S, Moretti M (2007) Importance of species abundance for assessment of trait composition: an example based on pollinator communities. *Community Ecol* 8:163–170.
- Bowen ME, McAlpine CA, House APN, Smith GC (2007) Regrowth forests on abandoned agricultural land: A review of their habitat values for recovering forest fauna. *Biol Conserv* 140: 273–296.
- Brose U, Jonsson T, Berlow EL, Warren P, Banasek-Richter C, Bersier L-F., Blanchard JL, Brey T, Carpenter SR, Blandenier M-FC, Cushing L, Dawah HA, Dell T, Edwards F, Harper-Smith S, Jacob U, Ledger ME, Martinez ND, Memmot, J, Mintenbeck K, Pinnegar JK, Rall BC, Rayner TS, Reuman DC, Ruess L, Ulrich W, Williams RJ, Woodward G, Cohen JE (2006) Consumer-resource body-size relationships in natural food webs. *Ecology* 87: 2411–2417.
- Buddle CM (2001) Spiders (Araneae) associated with downed woody material in a deciduous forest in central Alberta, Canada. *Agr Forest Entomol* 3: 241–251.
- Bultman TL, Uetz, GW, Brady AR (1982) A comparison of cursorial spider communities along a successional gradient. *J Arachnol* 10: 23–33.
- Buse J (2012) “Ghosts of the past”: flightless saproxylic weevils (Coleoptera: Curculionidae) are relict species in ancient woodlands. *J Insect Conserv* 16: 93–102.
- Cadotte MW, Carscadden K, Mirotchnick, N (2011) Beyond species: functional diversity and the maintenance of ecological processes and services: Functional diversity in ecology and conservation. *J Appl Ecol* 48: 1079–1087.
- Cardoso P, Pekár S, Jocqué R, Coddington JA (2011) Global Patterns of Guild Composition and Functional Diversity of Spiders. *PLoS ONE* 6: e21710.
- Cateau E, Larrieu L, Vallauri D, Savoie J-M, Touroult J, Brustel H (2015) Ancientness and maturity: two complementary qualities of forest ecosystems. *C R Biol* 338 : 58–73.

- 659 Chase JM (2003) Community assembly: when should history matter? *Oecologia* 136: 489–
660 498.
- 661 Davies GM, Gray A (2015) Don't let spurious accusations of pseudoreplication limit our
662 ability to learn from natural experiments (and other messy kinds of ecological monitoring).
663 *Ecol Evol* 5(22): 5295–5304.
- 664 Desender, K, Ervynck A, Tack G (1999) Beetle diversity and historical ecology of woodlands
665 in Flanders. *Belg J Zool* 129:139–156.
- 666 Dupouey J-L, Dambrine E, Laffite J-D, Moares C (2002) Irreversible impact of past land use
667 on forest soils and biodiversity. *Ecology* 83: 2978–2984.
- 668 Entling W, Schmidt MH, Bacher S, Brandl R, Nentwig W (2007) Niche properties of Central
669 European spiders: shading, moisture and the evolution of the habitat niche. *Global Ecol*
670 *Biogeogr* 16: 440–448.
- 671 Flinn KM, Marks PL (2007) Agricultural Legacies in Forest Environments: Tree
672 Communities, Soil Properties, and Light Availability. *Ecol Appl* 17: 452–463.
- 673 Fonseca CR, Ganade G (2001) Species functional redundancy, random extinctions and the
674 stability of ecosystems. *J Ecol* 89: 118–125.
- 675 Fukami T (2015) Historical Contingency in Community Assembly: Integrating Niches,
676 Species Pools, and Priority Effects. *Annu Rev Ecol Evol S* 46: 1-23.
- 677 Gallé R (2008) The effect of a naturally fragmented landscape on the spider assemblages.
678 *North-West J Zool* 4: 61–71.
- 679 Gallé R, Gallé-Szpisjak N, Torma A (2017) Habitat structure influences the spider fauna of
680 short-rotation poplar plantations more than forest age. *Eur J Forest Res* 136 : 51–58.
- 681 Gobbi M, Ballarin F, Brambilla M, Compostella M, Isaia M, Losapio G, Maffioletti C, Seppi
682 R, Tampucci D, Caccianiga M (2017) Life in harsh environments: carabid and spider trait
683 types and functional diversity on a debris-covered glacier and along its foreland. *Ecol*
684 *Entomol* 42 : 838 :848.
- 685 Goßner M, Engel K, Jessel B (2008) Plant and arthropod communities in young oak stands:
686 are they determined by site history? *Biodiver Conserv* 17: 3165–3180.
- 687 Gossner MM, Fonseca CR, Pašalić E, Türke M, Lange M, Weisser WW (2014) Limitations to
688 the use of arthropods as temperate forests indicators. *Biodiver Conserv* 23: 945–962.
- 689 Harvey PR, Nellist DR, Telfer MG (2002) Provisional Atlas of British Spiders (Arachnida,
690 Araneae), Biological Records Center. Huntington, UK.
- 691 Hermy M, Honnay O, Firbank L, Grashof-Bokdam C, Lawesson JE (1999) An ecological
692 comparison between ancient and other forest plant species of Europe, and the implications for
693 forest conservation. *Biol conserv* 91: 9–22.

- 694 Hermy M, Verheyen K (2007) Legacies of the past in the present-day forest biodiversity: a
695 review of past land-use effects on forest plant species composition and diversity. *Ecol Res* 22:
696 361–371.
- 697 Hobbs RJ, Higgs E, Hall C.M (2013) Novel ecosystems: intervening in the new ecological
698 world order. Wiley-Blackwell, Chichester, UK.
- 699 Hortal J, Borges PAV, Gaspar C (2006) Evaluating the performance of species richness
700 estimators: sensitivity to sample grain size. *J Anim Ecol* 75: 274–287.
- 701 Hurd LE, Fagan WF (1992) Cursorial spiders and succession: age or habitat structure?
702 *Oecologia* 92: 215–221.
- 703 Janssen P, Fuhr M, Cateau E, Nusillard B, Bouget C (2017) Forest continuity acts congruently
704 with stand maturity in structuring the functional composition of saproxylic beetles. *Biol*
705 *conserv* 205: 1–10.
- 706 Kirby K, Watkins C (2015) Europe's Changing Woods and Forests: From Wildwood to
707 Managed Landscapes. CAB Int, Wallingfor.
- 708 Laliberté E, Legendre P, Shipley B (2014) FD: measuring functional diversity from multiple
709 traits, and other tools for functional ecology. R package version 1.0-12.
- 710 Leitão RP, Zuanon J, Villéger S, Williams SE, Baraloto C, Fortune, C, Mendonça FP,
711 Mouillot D (2016) Rare species contribute disproportionately to the functional structure of
712 species assemblages. *P Roy Soc B-Bio Sci* 283: 20160084.
- 713 Leprieur F, Oikonomou A (2014) The need for richness-independent measures of turnover
714 when delineating biogeographical regions. *J Biogeogr* 41: 417–420.
- 715 Leroy B (2016) Rarity: Calculation of rarity indices for species and assemblages of species. R
716 package version 1-3-6.
- 717 Leroy B, Canard A, Ysnel F (2013) Integrating multiple scales in rarity assessments of
718 invertebrate taxa. *Divers Distrib* 19: 794–803.
- 719 Leroy, B, Petillon, J, Gallon, R, Canard, A, Ysnel, F, 2012 Improving occurrence-based rarity
720 metrics in conservation studies by including multiple rarity cut-off points: Multiple cut-offs in
721 rarity metrics. *Insect Conservation and Diversity* 5, 159–168.
- 722 Magura T, Bogyó D, Mizser S, Nagy DD, Tóthmérész B (2015) Recovery of ground-dwelling
723 assemblages during reforestation with native oak depends on the mobility and feeding habits
724 of the species. *Forest Ecol Manag* 339: 117–126.
- 725 Maire E, Grenouillet G, Brosse S, Villéger S (2015) How many dimensions are needed to
726 accurately assess functional diversity? A pragmatic approach for assessing the quality of
727 functional spaces: Assessing functional space quality. *Global Ecol Biogeogr* 24: 728–740.
- 728 Mallis RE, Hurd LE (2005) Diversity among ground-dwelling spider assemblages: habitat
729 generalists and specialists. *J Arachnol* 33: 101–109.

- 730 Marc P, Canard A, Ysnel F (1999) Spiders (Araneae) useful for pest limitation and
731 bioindication. *Agric Ecosyst Environ* 74: 229–273.
- 732 Miller JR, Bestelmeyer BT (2016) What’s wrong with novel ecosystems, really? *Restor Ecol*
733 24: 577–582.
- 734 Mouchet MA, Villéger S, Mason NWH, Mouillot D (2010) Functional diversity measures: an
735 overview of their redundancy and their ability to discriminate community assembly rules.
736 *Funct Ecol* 24, 867–876.
- 737 Mouillot D, Bellwood DR, Baraloto C, Chave J, Galzin R, Harmelin-Vivien M, Kulbicki M,
738 Lavergne S, Lavorel S, Mouquet N, Paine CET, Renaud J, Thuiller W (2013a) Rare Species
739 Support Vulnerable Functions in High-Diversity Ecosystems. *PLOS Biology* 11: e1001569.
- 740 Mouillot D, Graham NAI, Villéger S, Mason NWH, Bellwood DR (2013b) A functional
741 approach reveals community responses to disturbances. *Trends Ecol Evol* 28: 167–177.
- 742 Murcia C, Aronson J, Kattan GH, Moreno-Mateos D, Dixon K, Simberloff D (2014) A
743 critique of the ‘novel ecosystem’ concept. *Trends Ecol Evol* 29: 548–553.
- 744 Nentwig G (1986) Non-webbuilding spiders: prey specialists or generalists? *Oecol* 69: 571-
745 576.
- 746 Newbold T, Hudson LN, Hill SLL, Contu S, Lysenko I, Senior RA et al (2015) Global effects
747 of land use on local terrestrial biodiversity. *Nature*, 520: 45–50.
- 748 Nordén B, Dahlberg A, Brandrud TE, Fritz Ö, Ejrnaes R, Ovaskainen O (2014) Effects of
749 Ecological Continuity on Species Richness and Composition in Forests and Woodlands: A
750 Review. *Ecoscience* 21: 34–45.
- 751 Öberg S, Ekbom B, Bommarco R (2007) Influence of habitat type and surrounding landscape
752 on spider diversity in Swedish agroecosystems. *Agric Ecosyst Environ* 122: 211–219.
- 753 Oksanen J, Blanchet FG, M Friendly, Kindt R, Legendre P, McGlinn D, Minchin RB, O’Hara
754 RB, Simpson GL, Solymos P, Stevens MHH, Wagner ES, Wagner H (2017) *vegan*:
755 Community Ecology Package. R package version 2–4-4.
- 756 Pavoine S, Bonsall MB (2011) Measuring biodiversity to explain community assembly: a
757 unified approach. *Biol Rev* 86: 792–812.
- 758 Pearce JL, Venier LA (2006) The use of ground beetles (Coleoptera: Carabidae) and spiders
759 (Araneae) as bioindicators of sustainable forest management: A review. *Ecol Indic* 6: 780–
760 793.
- 761 Pearce JL, Venier LA, Eccles G, Pedlar J, MCKenney D (2005) Habitat Islands, Forest Edge
762 and Spring-active Invertebrate Assemblages. *Biodiver Conserv* 14: 2949–2969.
- 763 Pereira HM, Navarro LM (Eds.) (2015) *Rewilding European Landscapes*. Springer, New-
764 York.
- 765 Pinzon J, Wu L, He F, Spence JR (2018) Fine-scale forest variability and biodiversity in the
766 boreal mixedwood forest. *Ecography* 41: 753-769.

- Prieto-Benítez S, Méndez M (2011) Effects of land management on the abundance and richness of spiders (Araneae): a meta-analysis. *Biol Conserv* 144: 683–691.
- Queiroz C, Beilin R, Folke C, Lindborg R (2014) Farmland abandonment: threat or opportunity for biodiversity conservation? A global review. *Front Ecol Environ* 12: 288–296.
- R Core Team (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Renwick A, Jansson T, Verburg PH, Revoredo-Giha C, Britz W, Gocht A, McCracken D (2013) Policy reform and agricultural land abandonment in the EU. *Land Use Policy* 30: 446–457.
- Roberts MJ (1995) *Spiders of Britain & Northern Europe* Harper Collins, London; New York.
- Sala OE (2000) Global Biodiversity Scenarios for the Year 2100. *Science* 287: 1770–1774.
- Schaffers AP, Raemakers IP, Sýkora KV, Ter Braak CJ (2008) Arthropod assemblages are best predicted by plant species composition. *Ecology* 89: 782–794.
- Simpson GL (2016) permute: Functions for Generating Restricted Permutations of Data. R package version 0.9-4.
- Soberón J, Jiménez R, Golubov J, Koleff P (2007) Assessing completeness of biodiversity databases at different spatial scales. *Ecography* 30: 152–160.
- Spake R, Ezard THG, Martin PA, Newton AC, Doncaster CP (2015) A meta-analysis of functional group responses to forest recovery outside of the tropics. *Conserv Biol* 29: 1695–1703.
- Vavrek MJ, Vavrek MMJ (2011) fossil: palaeoecological and palaeogeographical analysis tools. *Palaeontol Electronica* 14:1T.
- Villéger S, Grenouillet G, Brosse S (2013) Decomposing functional β -diversity reveals that low functional β -diversity is driven by low functional turnover in European fish assemblages: Decomposing functional β -diversity. *Global Ecol Biogeogr* 22: 671–681.
- Villéger S, Mason NW, Mouillot D (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* 89: 2290–2301.
- Violle C, Thuiller W, Mouquet N, Munoz F, Kraft NJB, Cadotte MW, Livingstone SW, Mouillot D (2017) Functional Rarity: The Ecology of Outliers. *Trends Ecol Evol* 32: 356–367.
- Ziesche TM, Roth M (2008) Influence of environmental parameters on small-scale distribution of soil-dwelling spiders in forests: What makes the difference, tree species or microhabitat? *Forest Ecology and Management* 255: 738–752.

Figures captions

Fig. 1 Overview of the step-by-step analytical framework (see Materials and Methods for details).

Fig. 2 Ordination of the taxonomic and functional compositions of spider assemblages by principal coordinate analyse (PCoA) for the 56 assemblages (37 ancient forests and 19 recent woodlands). Overlap between spider communities of ancient forests (turquoise) and recent woodlands (red) is illustrated with one- (top and right of each graph) and two-dimensional kernel density (outer hull for 75%). The direction and the strength of the continuous environmental variables are represented by black arrows in each ordination (only significant variables; see Table 3). The strength of each variable is shown by the length of the arrow that is proportional to the correlation with ordination. The four symbols show the four identified groups of nearby sites (Online Resource 1).

Fig. 3 Structure, taxonomic and functional α -diversity of spider communities in ancient forests (n=37) and recent woodlands (n=19). Graphs show boxplots and means \pm standard errors. See methods for further details on the calculation of these indices.

Fig. 4 Composite view of conservation value of spider' communities of ancient forests and recent woodlands combining taxonomic indicators (a) and functional metrics (b,c,d). Graphs show both boxplots and mean \pm standard errors. See methods for further details on the calculation of these indices.

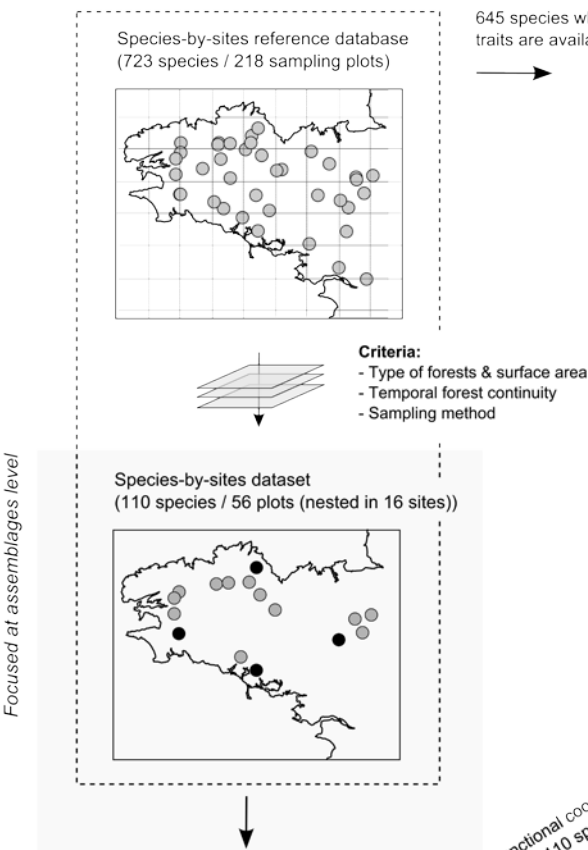
Fig. 5 Community-weighted mean (CWM) body size and proportion of presence-absence in each category for categorical traits of spider communities in ancient forests (n=37) and recent woodlands (n=19). Graphs show boxplots and means \pm standard errors. CWMs between the two forest categories were analysed with LMMs, except “Daily activity: Both”, “Guild: Orb web” and “Guild: Other hunters”, whose equivariance hypotheses were not validated and for which we performed GLMMs using Penalised Quasi-Likelihood (PQL).

Figures

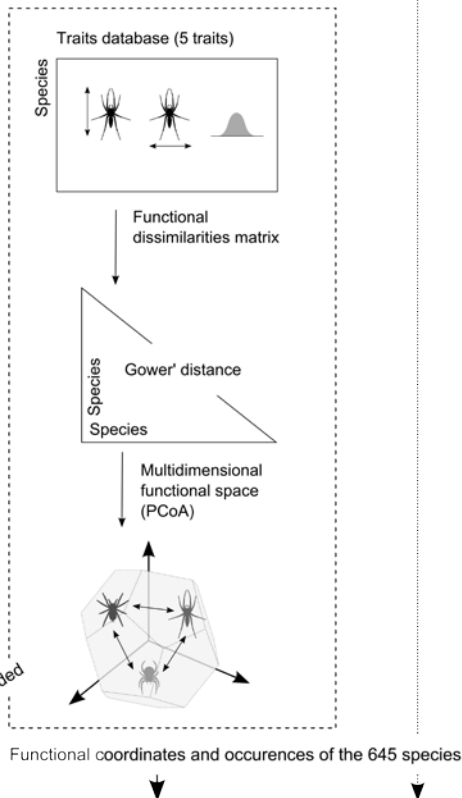
Figure 1

Step 1 : Selection & preparation of the dataset

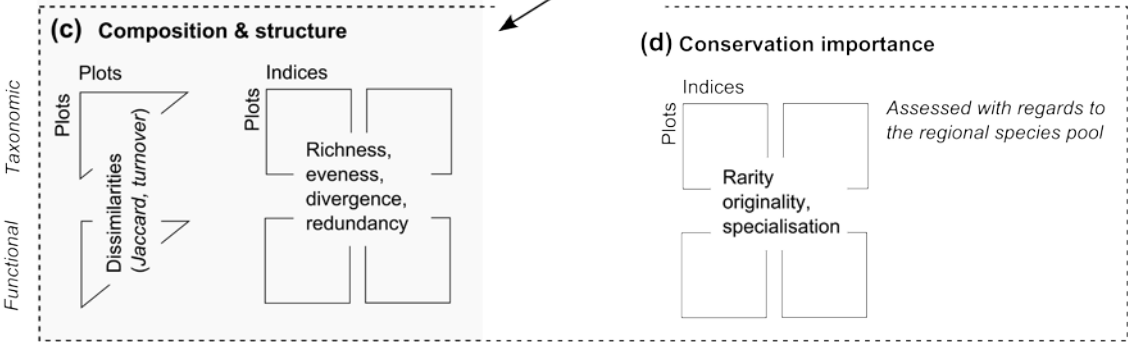
(a) Selection of species-by-sites dataset



(b) Functional distance between species



Step 2 : Calculation of the indices



Step 3 : Statistical treatments

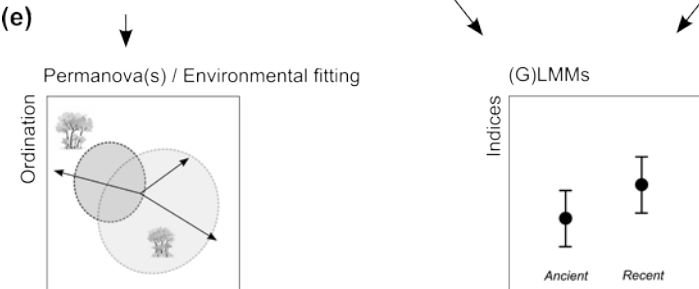


Figure 2

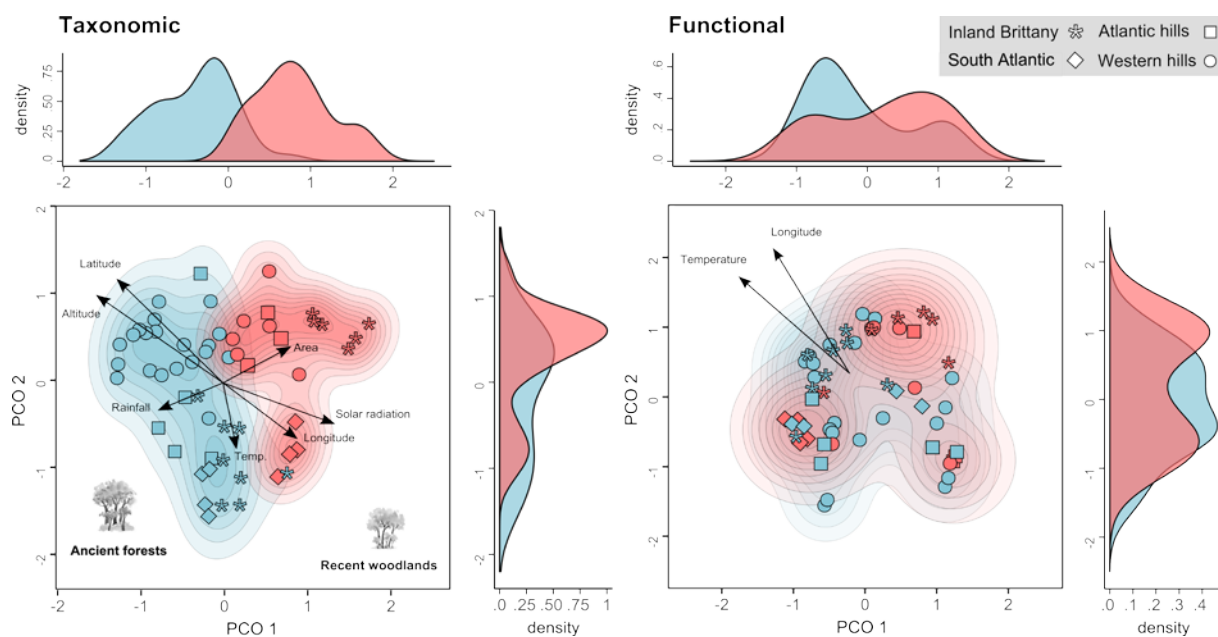


Figure 3

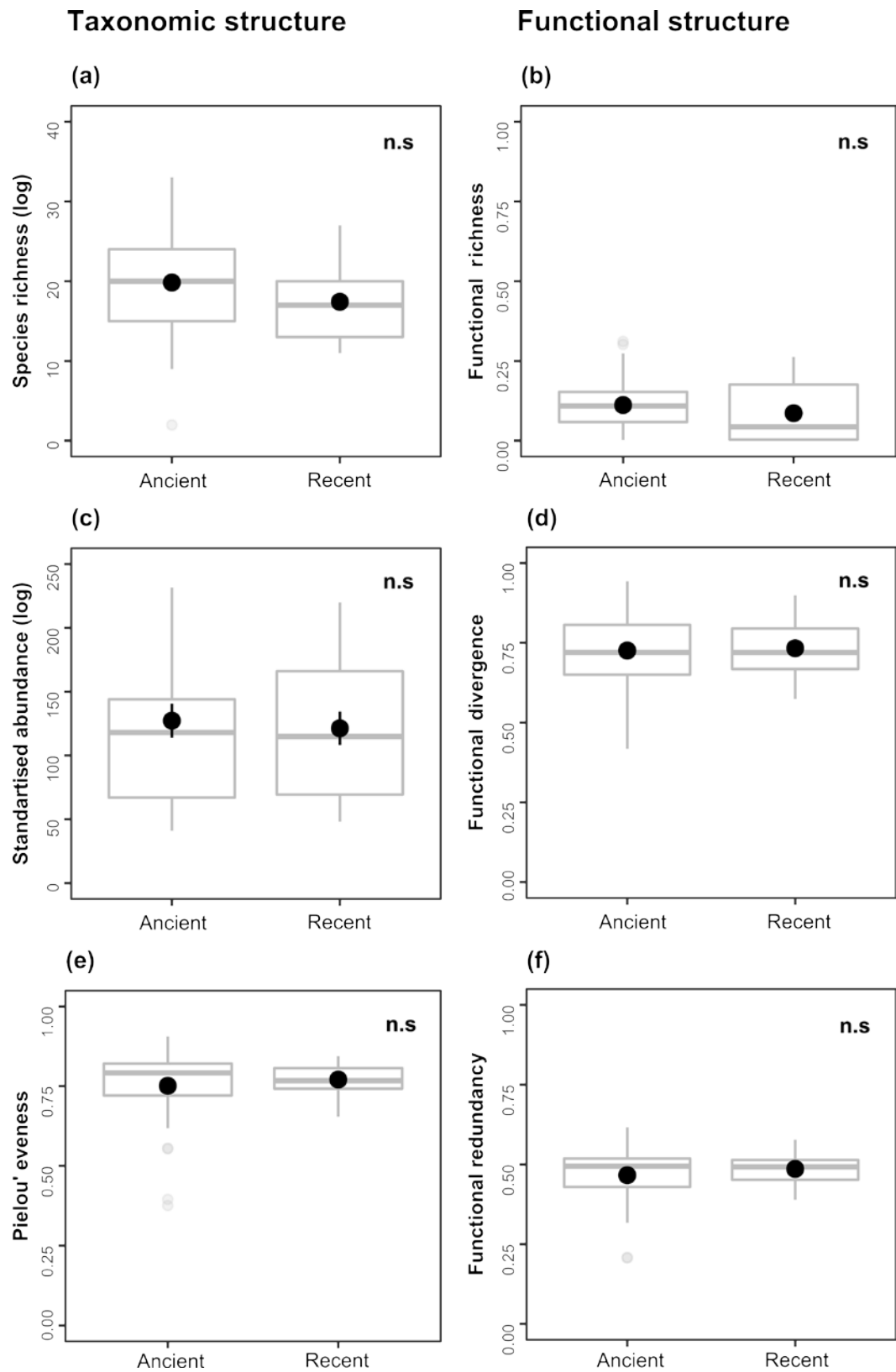


Figure 4

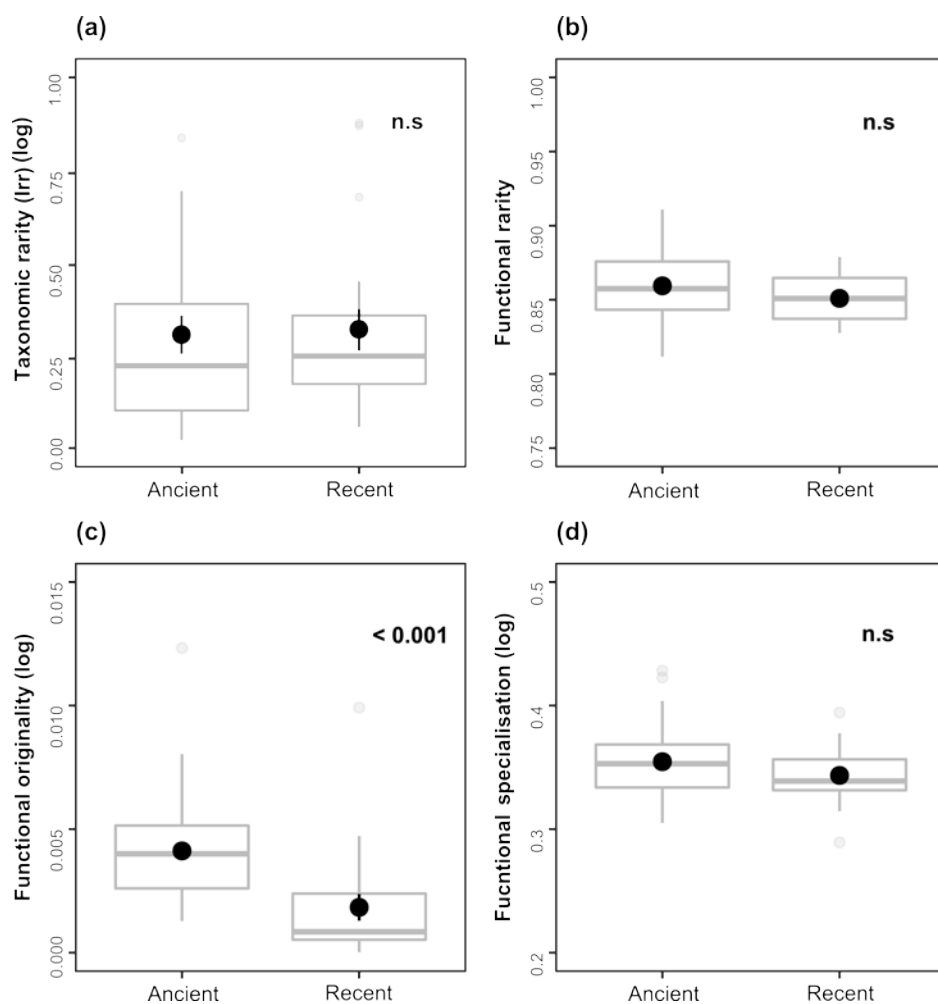
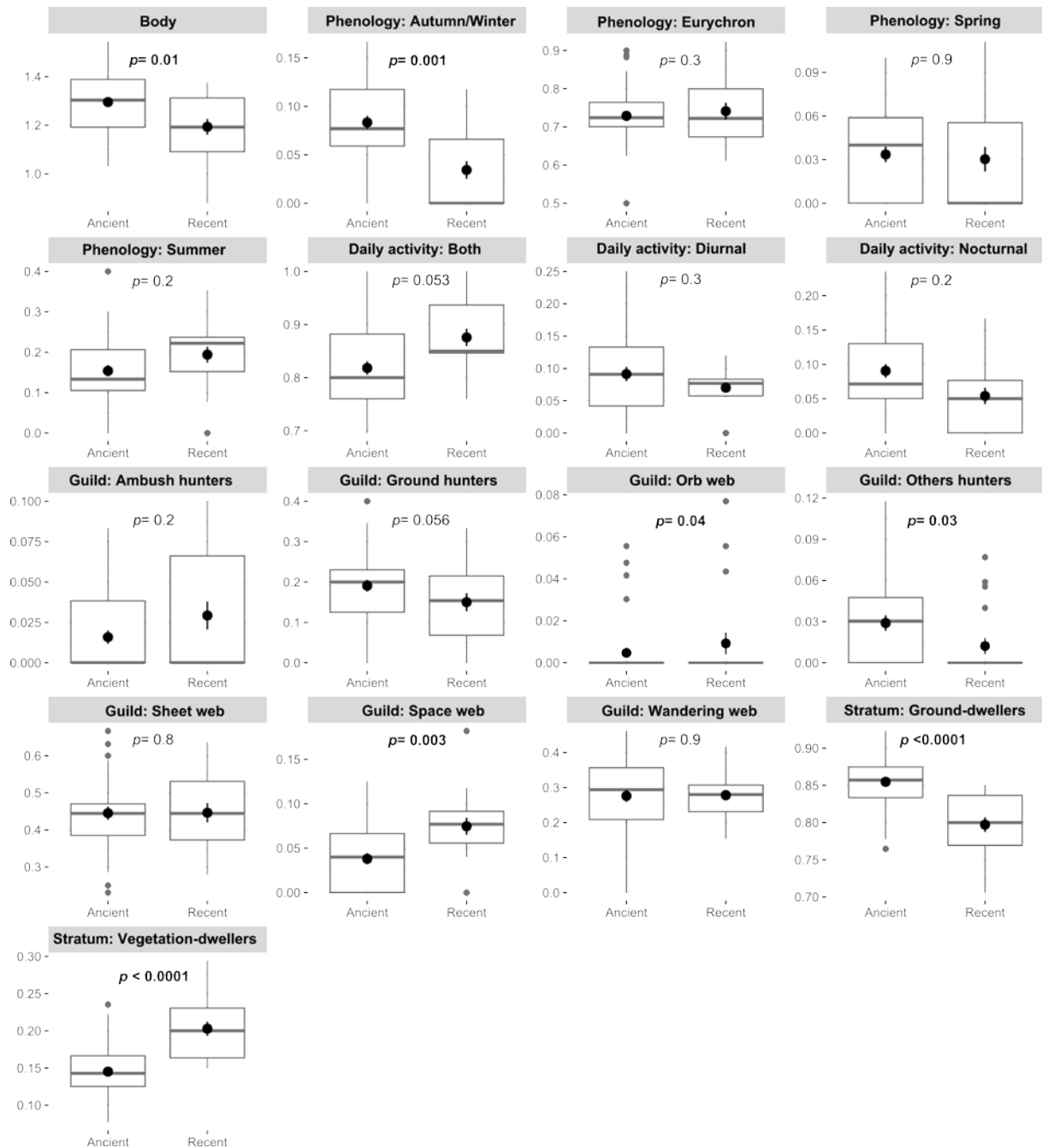


Figure 5



Tables

Table 1 Overview of the functional diversity indices used in the study at the α -level. While the first three indices analysed functional structure in each local community, FOr and FSpe were measured from the whole pool, i.e. the 645 species included in the functional space.

FD Component	Index	Measurement type	Weighted abundance	Influence of richness
Local communities				
Functional richness	FRic	the volume of multidimensional space occupied by all species in a community within a functional space	No	Yes
Functional divergence	FDiv	the proportion of total abundance supported by species with the most extreme trait values within a community	Yes	No
Functional redundancy	FR	difference between species diversity and Rao's quadratic entropy based on their functional dissimilarity	Yes	Yes
Whole regional pool				
Functional specialisation	FSpe	the mean distance of a species from the rest of the species pool in a functional space	Yes	No
Functional originality	FOr	the isolation of a species in the functional space occupied by a given community	Yes	No

Table 2 Summary of taxonomic and functional pairwise dissimilarities (Jaccard's index and Jaccard-derived dissimilarities) (i) within overall plots, (ii) within ancient and recent forests, (iii) between ancient and recent forests, and contribution of the turnover to each combination of pairwise dissimilarities. Values are mean \pm standard deviation with confidence interval at 95% in brackets.

	Taxonomic	Functional
Plot-to-plot variation		
Overall forests	0.71 \pm 0.09 [0.70 - 0.71]	0.79 \pm 0.17 [0.78 - 0.80]
Contribution of turnover	0.61 \pm 0.13 [0.61 - 0.62]	0.44 \pm 0.27 [0.43 - 0.46]
Ancient forests	0.68 \pm 0.09 [0.68 - 0.69]	0.76 \pm 0.19 [0.74 - 0.77]
Contribution of turnover	0.58 \pm 0.13 [0.57 - 0.59]	0.46 \pm 0.25 [0.44 - 0.48]
Recent woodlands	0.66 \pm 0.10 [0.65 - 0.68]	0.82 \pm 0.16 [0.80 - 0.85]
Contribution of turnover	0.56 \pm 0.14 [0.54 - 0.58]	0.40 \pm 0.26 [0.36 - 0.43]
β -diversity between ancient and recent forests		
Overall ancient vs. recent	0.74 \pm 0.8 [0.73 - 0.74]	0.81 \pm 0.16 [0.80 - 0.82]
Contribution of turnover	0.67 \pm 0.12 [0.65 - 0.67]	0.43 \pm 0.29 [0.41 - 0.46]

Table 3 Pearson's correlation coefficients of the nine environmental variables based on PCoA ordination (see Fig. 2); r^2 is the coefficient of determination and describes the goodness of fit, p refers to the significance of the correlation between the gradient and the PCoA scores, based on a random permutation ($n=9,999$). * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$.

	Taxonomic		Functional	
	r^2	p	r^2	p
Environmental variables				
Altitude	0.58	***	0.01	n.s.
Area of sites	0.14	*	0.11	n.s.
Latitude	0.54	***	0.03	n.s.
Longitude	0.20	**	0.18	**
Rainfall ₁₉₉₇₋₂₀₀₆	0.12	*	0.02	n.s.
Temperature maximum ₂₀₁₅	0.11	n.s.	0.18	**
Solar radiation ₁₉₉₇₋₂₀₀₆	0.34	***	0.01	n.s.
Geological substrate	0.14	***	0.11	n.s.
Temporal forest continuity	0.35	***	0.04	n.s.

SUPPLEMENTARY MATERIAL

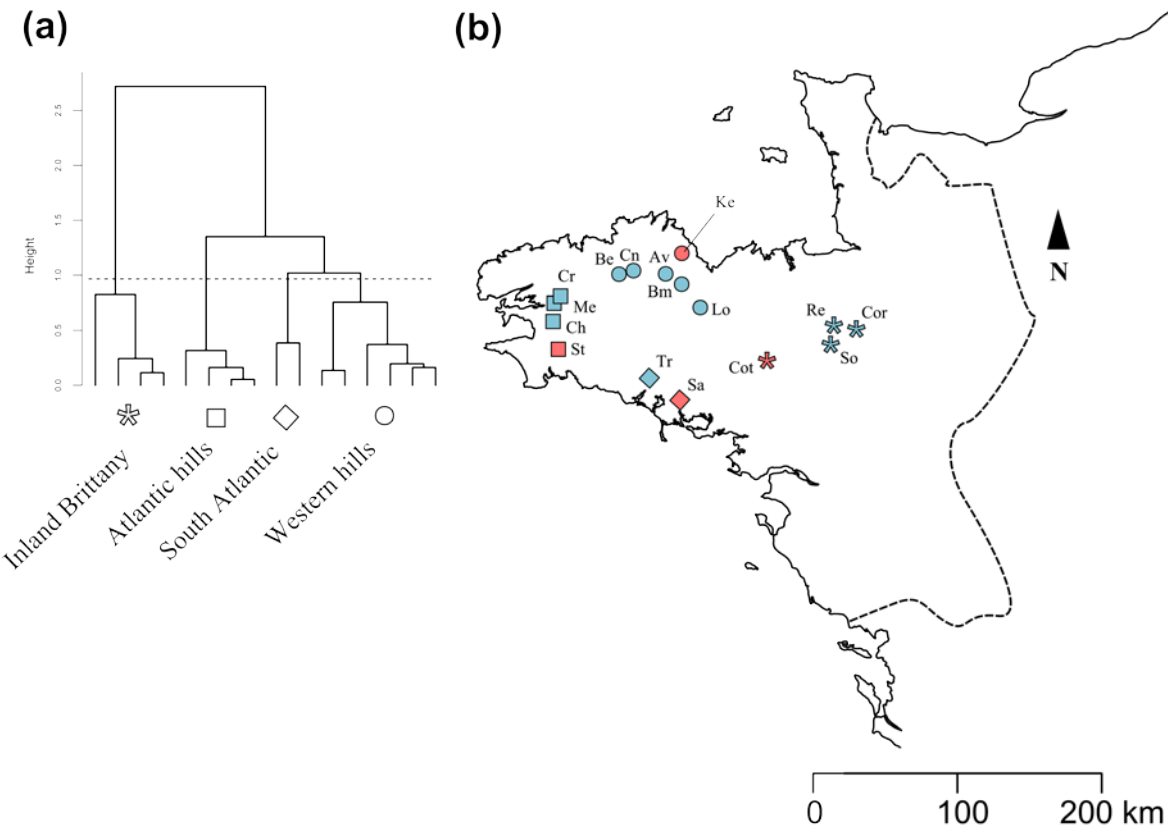
Authors: Loïs Morel¹, Benoît Dujol¹, Cyril Courtial¹, Manon Vasseur¹, Boris Leroy² and
Frédéric Ysnel¹

Title: Spontaneous recovery of functional diversity and rarity of ground-living spiders shed
light on the conservation importance of recent woodlands

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Online Resource 1



Spatial arrangement of the sampling design of the 16 study sites in the west of France. (a) Classification of each site based on their geographic positions (X and Y coordinates) (Euclidean distance, complete method); 4 groups of nearby sites were defined. (b) Map of the 16 study sites in the study region. See the table below for details of environmental features of each site and the specific sample design. Ancient forests are shown in turquoise, and recent woodlands in red.

1077 Summarised description of the forest sites according to the variables assessed at the site scale.

Sites	Abbreviation	No of plots	Geological substrate	Area (ha)	Altitude (m)	Sampling year
Avaugour	Av	6	Granite rock	1100	169	2013
Beaumanoir	Bm	3	Volcanic rock	300	214	2014
Beffou	Be	5	Volcanic rock	630	248	2014
Bois du Chap	Ch	2	Sandstone	40	91	2014
Coat-an-noz	Cn	3	Volcanic rock	1900	215	2014
Coetquidan	Cot	6	Sandstone	4000	97	2015
Corbières	Cor	3	Sandstone	630	101	2014
Cranou	Cr	2	Sandstone	1300	206	2014
Kério	Ke	6	Volcanic rock	200	94	2013
Lorges	Lo	3	Schist	2000	215	2014
Menez	Me	1	Sandstone	10	310	2014
Rennes	Re	3	Schist	3000	58	2014
Sal	Sa	4	Granite rock	52	32	2014
Soeuvres	So	2	Schist	115	54	2014
Stangala	St	3	Granite rock	57	59	2014
Tremelin	Tr	4	Granite rock	144	72	2014

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Online Resource 2

Arthropod sampling

In each plot, three pitfall traps consisting of polypropylene cups (10 cm diameter, 17 cm deep) with preservative solution (300 g.l⁻¹ of NaCl) (Spence and Niemela 1994), were placed at the middle of the plots and spaced out 10 m apart along a 20-m transect. This distance was considered to be the minimum distance to avoid interference between traps (Topping and Sunderland 1992). Trap size and type were selected based on Lange et al. (2011) to optimise arthropod sampling and limit the risk of trapping vertebrates involuntarily.

The 168 traps (56 plots x 3 traps) were collected fortnightly from April to June of 2013, or 2014, or 2015, and stored in 70% ethylalcohol. Only adults were considered for the studies.

Lange M, Gossner MM, Weissr WW (2011) Effect of pitfall trap type and diameter on vertebrate by-catches and ground beetle (Coleoptera: Carabidae) and spider (Araneae) sampling. *Methods Ecol Evol* 2: 185-190.

Spence JR, and Niemelä J (1994) Sampling carabid assemblages with pitfall traps: the madness and the method. *Can Entomol* 126: 881–894.

Topping CJ, Sunderland KD (1992) Limitations to the pitfall traps in ecological-studies exemplified by a study of spiders in a field of winter-wheat. *J Appl Ecol* 29: 485–491.

1109 **Online Resource 3**

1110 Trait data used to describe the functional features of the 110 species recorded in the dataset.

Family	Species	Body	Phenology	Daily activity	Hunting	Substrat
Agelenidae	<i>Coelotes terrestris</i>	13	Spring	Nocturnal	Sheet web	Surface
	<i>Eratigena picta</i>	7	Autumn-Winter	Both	Sheet web	Surface
	<i>Tegenaria silvestris</i>	7	Eurychron	Both	Sheet web	Surface
Amaurobiidae	<i>Amaurobius similis</i>	12	Eurychron	Nocturnal	Sheet web	Surface
Atypidae	<i>Atypus affinis</i>	15	Eurychron	Both	Ambush hunters	Surface
Clubionidae	<i>Clubiona comta</i>	6	Summer	Nocturnal	Other hunters	Vegetation
	<i>Clubiona terrestris</i>	7	Eurychron	Nocturnal	Other hunters	Surface
Dictynidae	<i>Cicurina cicur</i>	7	Eurychron	Both	Ground hunters	Surface
Dysderidae	<i>Dysdera erythrina</i>	10	Eurychron	Nocturnal	Ground hunters	Surface
	<i>Dysdera fuscipes</i>	3.2	Spring	Nocturnal	Ground hunters	Surface
	<i>Harpactea hombergi</i>	7	Eurychron	Nocturnal	Ground hunters	Vegetation
Gnaphosidae	<i>Drassyllus lutetianus</i>	7.5	Spring	Both	Ground hunters	Surface
	<i>Haplodrassus silvestris</i>	10	Summer	Both	Ground hunters	Surface
	<i>Trachyzelotes pedestris</i>	8	Summer	Both	Ground hunters	Surface
	<i>Zelotes apricorum</i>	9	Summer	Both	Ground hunters	Surface
Hahniidae	<i>Hahnia helveola</i>	3	Eurychron	Both	Sheet web	Surface
	<i>Hahnia ononidum</i>	2.5	Autumn-Winter	Both	Sheet web	Surface
	<i>Iberina montana</i>	2	Eurychron	Both	Sheet web	Surface
Linyphiidae	<i>Agneta ramosa</i>	2.5	Summer	Both	Sheet web	Surface
	<i>Bathyphantes gracilis</i>	2.5	Eurychron	Both	Sheet web	Surface
	<i>Centromerus albidus</i>	1.5	Eurychron	Both	Sheet web	Surface
	<i>Centromerus brevipalpus</i>	3	Autumn-Winter	Both	Sheet web	Surface
	<i>Centromerus dilutus</i>	1.5	Eurychron	Both	Sheet web	Surface
	<i>Centromerus serratus</i>	1.7	Eurychron	Both	Sheet web	Surface
	<i>Centromerus sylvaticus</i>	4	Eurychron	Both	Sheet web	Surface
	<i>Ceratinella scabrosa</i>	2.3	Summer	Both	Wandering web	Surface
	<i>Dicymbium tibiale</i>	2.6	Eurychron	Both	Wandering web	Surface
	<i>Diplocephalus cristatus</i>	2.5	Eurychron	Both	Wandering web	Surface
	<i>Diplocephalus latifrons</i>	2	Eurychron	Both	Wandering web	Surface
	<i>Diplocephalus picinus</i>	1	Summer	Both	Wandering web	Surface
	<i>Diplostyla concolor</i>	3	Eurychron	Both	Sheet web	Surface
	<i>Erigone atra</i>	2.8	Eurychron	Both	Wandering web	Surface
	<i>Erigone dentipalpis</i>	2.6	Eurychron	Both	Wandering web	Surface
	<i>Gonatium rubellum</i>	3.4	Eurychron	Both	Wandering web	Surface
	<i>Gongylidiellum latebricola</i>	1.9	Summer	Both	Wandering web	Surface
	<i>Gongylidiellum vivum</i>	1.9	Eurychron	Both	Wandering web	Surface
	<i>Gongylidium rufipes</i>	3.7	Summer	Both	Wandering web	Surface
	<i>Jacksonella falconeri</i>	1.2	Eurychron	Both	Wandering web	Surface
	<i>Labulla thoracica</i>	6.4	Eurychron	Both	Sheet web	Vegetation
	<i>Linyphia hortensis</i>	5	Spring	Both	Sheet web	Vegetation
	<i>Macrargus rufus</i>	4.6	Eurychron	Both	Sheet web	Surface

	<i>Maro minutus</i>	1.5	Eurychron	Both	Sheet web	Surface
	<i>Maso sundevalli</i>	1.8	Eurychron	Both	Wandering web	Vegetation
	<i>Micrargus apertus</i>	2.2	Eurychron	Both	Wandering web	Surface
	<i>Micrargus herbigradus</i>	1.9	Eurychron	Both	Wandering web	Surface
	<i>Microneta viaria</i>	3	Eurychron	Both	Sheet web	Surface
	<i>Minyriolus pusillus</i>	1.3	Spring	Both	Wandering web	Surface
	<i>Monocephalus fuscipes</i>	2.2	Eurychron	Both	Wandering web	Surface
	<i>Neriene clathrata</i>	5	Eurychron	Both	Sheet web	Vegetation
	<i>Oedothorax apicatus</i>	3.3	Eurychron	Both	Wandering web	Surface
	<i>Oedothorax retusus</i>	3	Eurychron	Both	Wandering web	Surface
	<i>Ostearius melanopygius</i>	2.6	Eurychron	Both	Wandering web	Surface
	<i>Palliduphantes pallidus</i>	2.3	Eurychron	Both	Sheet web	Vegetation
	<i>Parapelecopsis nemoralis</i>	2.1	Eurychron	Both	Wandering web	Surface
	<i>Pocadicnemis pumila</i>	2.2	Spring	Both	Wandering web	Surface
	<i>Saaristoia abnormis</i>	4	Eurychron	Both	Sheet web	Surface
	<i>Saloca diceros</i>	1.4	Autumn-Winter	Both	Sheet web	Surface
	<i>Sintula corniger</i>	2	Eurychron	Both	Wandering web	Surface
	<i>Tapinocyba mitis</i>	1.5	Autumn-Winter	Both	Wandering web	Surface
	<i>Tenuiphantes cristatus</i>	2.8	Autumn-Winter	Both	Sheet web	Vegetation
	<i>Tenuiphantes flavipes</i>	2.5	Eurychron	Both	Sheet web	Vegetation
	<i>Tenuiphantes tenuis</i>	3.2	Eurychron	Both	Sheet web	Vegetation
	<i>Tenuiphantes zimmermanni</i>	3.2	Eurychron	Both	Sheet web	Vegetation
	<i>Tiso vagans</i>	2.2	Eurychron	Both	Wandering web	Surface
	<i>Trichoncus affinis</i>	2.5	Eurychron	Both	Wandering web	Surface
	<i>Walckenaeria acuminata</i>	4	Eurychron	Both	Wandering web	Surface
	<i>Walckenaeria atrotibialis</i>	2.8	Summer	Both	Wandering web	Surface
	<i>Walckenaeria corniculans</i>	3	Eurychron	Both	Wandering web	Surface
	<i>Walckenaeria cucullata</i>	2.7	Eurychron	Both	Wandering web	Surface
	<i>Walckenaeria cuspidata</i>	2.9	Eurychron	Both	Wandering web	Surface
	<i>Walckenaeria dysderoides</i>	2.2	Spring	Both	Wandering web	Surface
	<i>Walckenaeria incisa</i>	3.2	Eurychron	Both	Wandering web	Surface
	<i>Walckenaeria mitrata</i>	3.3	Spring	Both	Wandering web	Surface
	<i>Walckenaeria nudipalpis</i>	2.7	Eurychron	Both	Wandering web	Surface
	<i>Walckenaeria obtusa</i>	3.8	Eurychron	Both	Wandering web	Surface
	<i>Wiehlea calcarifera</i>	1.3	Eurychron	Both	Wandering web	Surface
Liocranidae	<i>Agroeca brunnea</i>	8	Eurychron	Both	Ground hunters	Surface
	<i>Apostenus fuscus</i>	4	Eurychron	Both	Ground hunters	Surface
	<i>Scotina celans</i>	4.7	Eurychron	Both	Ground hunters	Surface
Lycosidae	<i>Alopecosa pulverulenta</i>	10	Summer	Diurnal	Ground hunters	Surface
	<i>Hygrolycosa rubrofasciata</i>	6	Spring	Diurnal	Ground hunters	Surface
	<i>Pardosa amentata</i>	8	Summer	Diurnal	Ground hunters	Surface
	<i>Pardosa hortensis</i>	5.5	Summer	Diurnal	Ground hunters	Surface
	<i>Pardosa prativaga</i>	6	Summer	Diurnal	Ground hunters	Surface
	<i>Pardosa proxima</i>	6.5	Summer	Diurnal	Ground hunters	Surface
	<i>Pardosa pullata</i>	6	Eurychron	Diurnal	Ground hunters	Surface
	<i>Pardosa saltans</i>	5.7	Summer	Diurnal	Ground hunters	Surface
	<i>Pirata uliginosus</i>	6	Summer	Diurnal	Ground hunters	Surface

	<i>Piratula hygrophila</i>	6.5	Summer	Diurnal	Ground hunters	Surface
	<i>Piratula latitans</i>	5	Summer	Diurnal	Ground hunters	Surface
	<i>Trochosa ruricola</i>	14	Eurychron	Diurnal	Ground hunters	Surface
	<i>Trochosa terricola</i>	14	Eurychron	Diurnal	Ground hunters	Surface
Miturgidae	<i>Zora spinimana</i>	6.5	Eurychron	Both	Ground hunters	Surface
Phrurolithidae	<i>Phrurolithus festivus</i>	3	Summer	Both	Ground hunters	Surface
Salticidae	<i>Neon reticulatus</i>	3	Eurychron	Diurnal	Other hunters	Surface
Tetragnathidae	<i>Metellina mengei</i>	6	Summer	Both	Orb web	Vegetation
	<i>Pachygnatha clercki</i>	7	Eurychron	Both	Orb web	Surface
	<i>Pachygnatha degeeri</i>	3.7	Eurychron	Both	Orb web	Surface
Theridiidae	<i>Enoplognatha thoracica</i>	4	Eurychron	Both	Space web	Surface
	<i>Euryopsis flavomaculata</i>	4	Summer	Both	Space web	Surface
	<i>Pholcomma gibbum</i>	1.5	Eurychron	Both	Space web	Surface
	<i>Robertus lividus</i>	4	Eurychron	Both	Space web	Surface
	<i>Theonoe minutissima</i>	1.2	Eurychron	Both	Space web	Surface
	<i>Theridion mystaceum</i>	2.5	Summer	Both	Space web	Vegetation
Thomisidae	<i>Cozyptila blackwalli</i>	4	Eurychron	Both	Ambush hunters	Surface
	<i>Ozyptila praticola</i>	4	Eurychron	Both	Ambush hunters	Surface
	<i>Ozyptila trux</i>	5	Eurychron	Both	Ambush hunters	Surface
	<i>Xysticus cristatus</i>	8	Summer	Both	Ambush hunters	Vegetation
	<i>Xysticus luctator</i>	10	Summer	Both	Ambush hunters	Surface
Zodariidae	<i>Zodarion italicum</i>	3	Summer	Both	Ambush hunters	Surface

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1124 **Online Resource 4**

1125 Species richness, richness estimator and completeness of each site of the datasets. Completeness is the
 1126 ratio between observed and estimated richness (Soberón et al., 2007). For each site, completeness was
 1127 based on three estimators (Chao2, Jackknife 1 and ICE). For species richness and completeness values
 1128 are means \pm standard errors.

	No of plots	Total richness	Mean species richness \pm se	Chao2	Jackknife 1	ICE	Completeness index \pm se
Overall datasets	56	110	19.02 \pm 0.75	0.80	0.91	0.79	0.83 \pm 0.04
Recent woodlands	19	71	17.42 \pm 1.12	0.49	0.85	0.70	0.68 \pm 0.11
Coetquidan	6	32	16 \pm 1.15	0.80	0.78	0.91	0.83 \pm 0.04
Kério	6	38	17.33 \pm 1.61	0.73	0.73	0.87	0.78 \pm 0.05
Sal	4	41	23.75 \pm 1.97	0.77	0.73	0.84	0.78 \pm 0.03
Stangala	3	21	12 \pm 0.58	0.63	0.66	0.69	0.66 \pm 0.02
Ancient forests	37	101	19.84 \pm 0.95	0.72	0.87	0.75	0.78 \pm 0.05
Avaugour	6	28	13.33 \pm 1.05	0.86	0.78	0.90	0.85 \pm 0.04
Beaumanoir	3	29	19.67 \pm 0.88	0.82	0.75	0.83	0.80 \pm 0.03
Beffou	5	45	21.8 \pm 1.88	0.79	0.74	0.85	0.80 \pm 0.03
Bois du Chap	2	19	-	-	-	-	-
Coat-an-noz	3	32	21.33 \pm 4.33	0.69	0.71	0.80	0.74 \pm 0.03
Corbières	3	37	21.33 \pm 1.33	0.72	0.68	0.72	0.70 \pm 0.01
Cranou	2	46	-	-	-	-	-
Lorges	3	24	16 \pm 0.58	0.78	0.73	0.81	0.77 \pm 0.02
Menez	1	13	-	-	-	-	-
Rennes	3	49	28 \pm 2.65	0.61	0.66	0.69	0.65 \pm 0.02
Soeuvres	2	33	-	-	-	-	-
Tremelin	4	40	22 \pm 3.03	0.87	0.76	0.85	0.83 \pm 0.04

1130 **Online Resource 5**

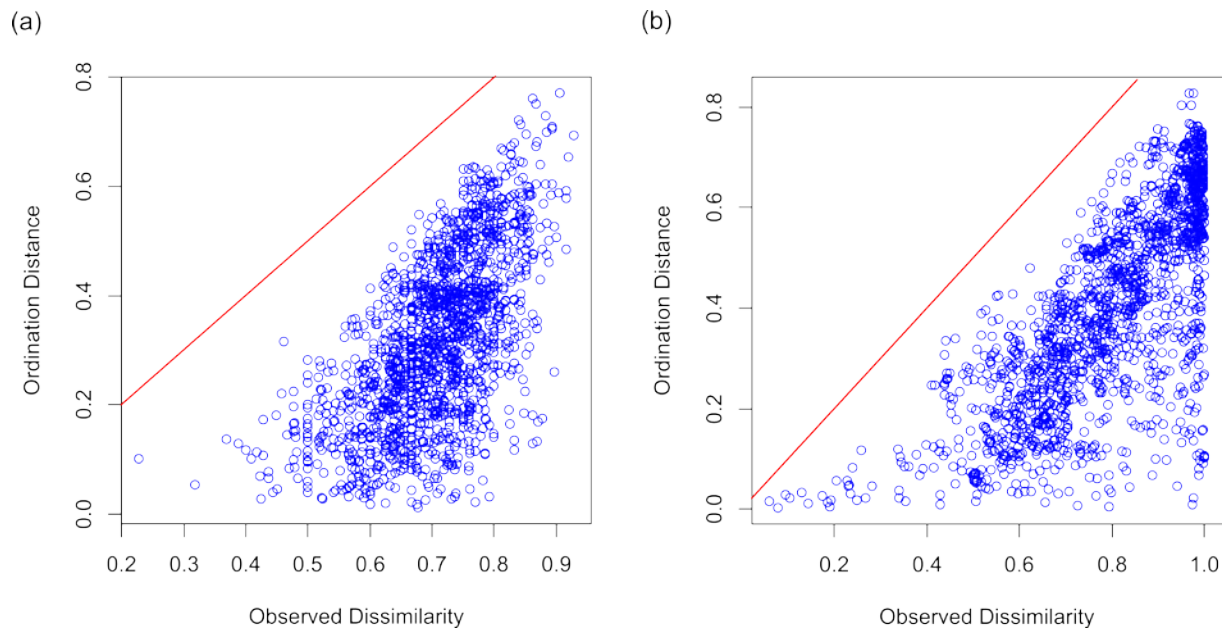
1131 Summary of the statistical tests for all the indices used to analyse differences in structure,
 1132 taxonomic and functional α -diversity of spider communities of ancient forests and recent
 1133 woodlands.

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Metrics	Ancient forests	Recent woodlands	Wald's test	<i>p</i>
Species richness	19.8 ± 0.95	17.4 ± 1.11	1.4	0.24
Standardised abundance (log)	127.2 ± 13.4	121.3 ± 13.1	0.04	0.85
Pielou' eveness	0.75 ± 0.02	0.77 ± 0.02	0.6	0.44
FRic	0.12 ± 0.01	0.08 ± 0.02	3.12	0.08
FDiv	0.72 ± 0.02	0.74 ± 0.02	0.11	0.73
FR	0.46 ± 0.01	0.47 ± 0.01	0.19	0.66
<i>I_{RR}</i> (log)	0.30 ± 0.05	0.32 ± 0.06	0.16	0.69
FRar	0.86 ± 0.004	0.85 ± 0.004	1.43	0.23
FOri (log)	0.007 ± 0.001	0.004 ± 0.001	12.9	0.0003
FSpe	0.36 ± 0.01	0.36 ± 0.01	0.4	0.53
CWM _{Body}	1.3 ± 0.2	1.19 ± 0.03	6.7	0.01
CWM _{Phenology: Autumn/Winter}	0.08 ± 0.01	0.03 ± 0.01	11.4	0.0007
CWM _{Phenology: Eurychron}	0.73 ± 0.01	0.74 ± 0.02	1.06	0.30
CWM _{Phenology: Spring}	0.03 ± 0.01	0.03 ± 0.01	0.01	0.92
CWM _{Phenology: Summer}	0.15 ± 0.01	0.19 ± 0.02	1.56	0.21
CWM _{Daily activity: Both}	0.82 ± 0.01	0.88 ± 0.02	3.74	0.05
CWM _{Daily activity: Diurnal}	0.09 ± 0.01	0.07 ± 0.01	1.21	0.27
CWM _{Daily activity: Nocturnal}	0.09 ± 0.01	0.05 ± 0.01	1.32	0.25
CWM _{Guild: Ambush hunters}	0.16 ± 0.004	0.03 ± 0.01	1.39	0.24
CWM _{Guild: Ground hunters}	0.19 ± 0.01	0.15 ± 0.02	3.63	0.056
CWM _{Guild: Orb web}	0.005 ± 0.002	0.01 ± 0.01	4.34	0.03
CWM _{Guild: Others hunters}	0.03 ± 0.01	0.01 ± 0.01	4.75	0.03
CWM _{Guild: Sheet web}	0.45 ± 0.02	0.45 ± 0.03	0.09	0.76
CWM _{Guild: Space web}	0.04 ± 0.01	0.07 ± 0.01	8.94	0.003
CWM _{Guild: Wandering web}	0.28 ± 0.02	0.28 ± 0.01	0.01	0.92
CWM _{Stratum: Ground-dwellers}	0.85 ± 0.01	0.8 ± 0.01	16.9	< 0.0001
CWM _{Stratum: Vegetation-dwellers}	0.16 ± 0.01	0.2 ± 0.01	16.9	< 0.0001

Online Resource 6

Shepard diagrams showing the goodness of fit of the measured pairwise dissimilarities of the spider assemblages as compared to the pairwise dissimilarities represented by PCoA ordination, for the taxonomic level (a) and the functional level (b).



Online Resource 7

Table representing the distribution of the 110 spider species between ancient forests and recent woodlands with their weight of functional originality (a) and specialisation (b) assessed from the functional space (see Table 1 for details of metrics). Coloured circles represent abundance standardised based on the number of days a trap was active. Grey circles represent the frequency of the species in each forest category (e.g. 0.25 for ancient forests, i.e. one species observed in 9/37 plots).

